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A large Jurassic pterodactyloid in northern France and a review of the French Pterosaur record

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Key words. – Pterosauria, Mesozoic, France, Extinctions.

Abstract. – A very large mandible from the Jurassic (Lower Tithonian) of the Boulogne-sur-Mer area (Pas-de-Calais, France) is described. The specimen does not allow a precise identification but could be close to *Gallodactylus canjuersensis* within the Pterodactylidae. A tentative wingspan estimation of the taxon gives us a figure of about 2.5 m, which, if correct, would make it a remarkably large pterosaur for that time. An exhaustive review of the French pterosaur record is also presented. Although few remarkable finds have been reported, pterosaurs are known in France from a number of sites ranging in age from the late Triassic to the uppermost Cretaceous. The French record shows that the pterosaur stratigraphical concentrations are unlikely to be related to actual pterosaur palaeoecological importance during the Mesozoic. The apparent diversity of this group through time constitutes therefore a very unsuitable element to bring arguments, in either one way or another, to the mass extinction debate.

Un grand Pterodactyloidea jurassique dans le Nord de la France et une revue des ptérosaures de France

Mots clés. – Pterosauria, Mésozoïque, France, Extinctions.

Résumé. – Le Jurassique supérieur (Tithonien inférieur) près du « Cran aux Œufs » (Boulonnais, Pas-de-Calais, France) a livré une très grande mandibule de Pterodactyloidea (longueur initiale estimée : 227 mm).

Le spécimen, de par son état, ne permet pas une détermination systématique précise. Il pourrait former, avec *Gallodactylus canjuersensis* (Tithonien inférieur, Canjuers, Var, France), un clade (basé sur la synapomorphie putative « absence de dents sur le dentaire ») au sein des Pterodactylidae (*Pterodactylus antiquus*, *Ctenochasma elegans*, leur ancêtre commun le plus récent et tous ses descendants).

Une estimation, naturellement très approximative, de l'envergure originale du taxon donne 2,5 m ce qui fait de celui-ci un ptérosaure remarquablement grand pour le Jurassique.

Le registre fossile français atteste la présence de ptérosaures depuis le Trias supérieur (Rhétien) jusqu'au Crétacé terminal (Maastrichtien supérieur). Les étages Kimméridgien-Tithonien et, dans une moindre mesure, Albien et Maastrichtien, sont les moins pauvres à cet égard.

Cette apparente variation locale de l'importance du groupe au cours du temps est cependant sans signification biologique. Elle pourrait être liée à des biais concernant la richesse relative de certains gisements particuliers (Kimméridgien- Tithonien), la durée particulièrement longue d'un étage (Albien) ou l'exploitation paléontologique préférentielle d'un autre (Maastrichtien).

La diversité apparente des ptérosaures au cours du Mésozoïque constitue une donnée délétère dans les débats sur les phénomènes d'extinctions en masse.

INTRODUCTION

French pterosaurs, although mentioned as early as the mid-nineteenth century, have been the subject of relatively few papers. This is not surprising in view of the fact that the material is rare and, more often than not, discrete. However, in recent years, several papers have dealt with interesting pterosaur remains from the French Jurassic as well as from the Cretaceous. Besides skeletal elements [Buffetaut *et al.*, 1996; Buffetaut *et al.*, 1997; Buffetaut *et al.*, 1998], highly remarkable trackways have been the subject of noteworthy studies [Mazin *et al.*, 1995; Mazin *et al.*, 1997].

The discovery of an extremely large pterosaurian mandible in northern France as well as new other remarkable remains from the Jurassic and Cretaceous of the same area and one isolated pterosaur tooth from Normandy in the collection of the Muséum national d'Histoire naturelle (Paris) is the motivation to make an inventory of all the pterosaur material attested so far in France (fig. 1).

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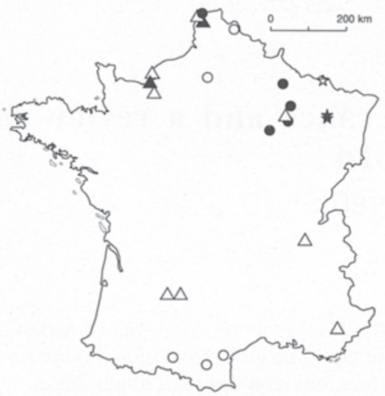

FIG. 1. – Geographical distribution of the French pterosaur localities (see text). Black stars : Upper Triassic; white star : Lower Jurassic; black triangles : Middle Jurassic; white triangles : Upper Jurassic; black circles : Lower Cretaceous; white circles : Upper Cretaceous.

FIG. 1. – *Répartition géographique des sites français ayant livré des ptérosaures (voir le texte). Etoiles noires : Trias supérieur ; étoile blanche : Jurassique inférieur ; triangles noirs : Jurassique moyen ; triangles blancs : Jurassique supérieur ; disques noirs : Crétacé inférieur ; disques blancs : Crétacé supérieur.*

THE LARGE PTEROSAUR OF THE BOULOGNE-SUR-MER AREA

Description

Order Pterosauria KAUP, 1834
Suborder Pterodactyloidea PLIENINGER, 1901
Family ? Pterodactylidae BONAPARTE, 1838
Gen. et sp. indet.

Recently, the Jurassic of the Boulogne-sur-Mer area (Pas-de-Calais, northern France) has yielded an incomplete pterosaurian mandible (fig. 2) found by one of the authors (A. B.). More accurately, the specimen comes from a rock fallen from the cliffs between 'Cran aux Œufs' and 'Cran Barbier', near the Cape Gris-Nez. The original layer of the specimen was the 'Grès de la Crèche inférieurs' of Lower Tithonian age [Debrand-Passard and Rioult, 1980; Geyssant *et al*., 1993].

The specimen belongs to the Bouveur collection (Saint-Omer, Pas-de-Calais). A cast of it is kept in the collection of the Laboratoire de Paléontologie, Muséum national d'Histoire naturelle (Paris), under the number of entry 2000-8.

The specimen appears on the dorsal side in the matrix. The rostralmost part is missing but has left an accurate imprint in the sandstone. The break allows us to see a hollow mandible with little more than a 1 mm thick bone lining at this place. The two branches of the mandible diverge at an angle of about 12°. No tooth or trace of tooth sockets, on either the bone or the matrix, is visible. Unfortunately, due to the fragility of the specimen, its further preparation cannot be envisaged. However, a radiograph was made and has not shown any additional character.

The individual is extremely large in comparison with most Lower Tithonian Solnhofen pterodactyloids [Wellnhofer, 1970]. However, there are postcranial elements of large pterodactyloids, such as '*Pterodactylus*' *grandis* [Cuvier, 1824] and others, that might match this size [Wellnhofer, pers. comm. to F. K., 1999]. Unfortunately, these pterodactyloids are little known and could merely be larger specimens of better documented taxa.

The mandible length was 227 mm and an extremely tentative wing span estimation by extrapolation from well known Pterodactylidae, such as *Ctenochasma elegans* and *Cycnorhamphus suevicus*, gives about 2.5 m (viz. nearly that of a bearded vulture). The same wing span has been estimated [Wellnhofer, 1991] for '*Pterodactylus*' *grandis* (mentioned in France at Cerin, see below) as well as for the roughly contemporary pterodactyloid *Kepodactylus insperatus* of Colorado [Harris and Carpenter, 1996] and 'rhamphorhynchoid' *Comodactylus ostromi* of Wyoming [Galton, 1981] (the 'Rhamphorhynchoidea' being very probably paraphyletic the name is used herein *sensu* Unwin [1995]). All three were considered as the largest known Jurassic pterosaurs. However, a bone from the Kimmeridgian of northern Switzerland, initially referred to a theropod [Huene, 1926], was recently reinterpreted as the second phalanx of the wing digit IV of a pterodactyloid, with a possible wingspan in excess of 4 m [Meyer and Hunt, 1989]. Likewise, the identification of *Purbeckopus* as a pterosaur track shows that very large pterosaurs had already appeared by the end of the Jurassic [Wright *et al*., 1997].

Systematics

The somewhat older '*Pterodactylus*' *suprajurensis* from the same area (see below) is known only by postcranial material. Wellnhofer [1978, 1980] considered '*Pterodactylus*' *grandis* as a Pterodactylidae of uncertain systematic position. The rather large, but by far smaller, pterodactyloid from Canjuers (see below) is now finally considered to have been toothless (cf. Fabre *et al*. [1982], followed by Ginsburg [1983] but ignored by Bennett [1996a] and Jouve [2000]).

Only certain pterodactyloid groups have jaws not (or partially) armed with teeth and the absence of teeth is very rare amongst Jurassic pterosaurs. According to Unwin and Lü [1997], toothlessness *per se* is not a reliable guide to the general relationships of pterodactyloids but is informative at a more exclusive level. This character needs to be confirmed but could therefore well be a synapomorphy of *Gallodactylus canjuersensis* and this new specimen from the Boulogne-sur-Mer area. Nevertheless, this cannot be affirmed without a detailed character analysis that is impossible to conduct satisfactorily due to the state of the specimens.

However, the zone of the 'glenoid cavity' [Fabre, 1974, Fig. 2] is remarkably similar in both specimens. Yet, Fabre [1974, 1976] reconstructed the mandible as ventrally curved but this character is probably artifactual as already suggested by Bennett [1996a]. If, likewise, the difference in size is related to different growth stages (the specimen from Canjuers being immature according to Bennett [1996a] *contra* Fabre [1974, 1976]) the possibility of a single species for both specimens cannot be excluded.

Gallodactylus has been assigned to the Pterodactylidae by Fabre [1974, 1976] and Wellnhofer [1978, 1980] but to the 'Gallodactylidae' by Wellnhofer [1991]. Contrary to Wellnhofer [1991, p. 185], followed by Benton [1993, p. 700], Fabre [1974] never erected the 'Gallodactylidae' nor another taxon of the family group *Gallodactylus* should therefore be retained, for the time being, in the Pterodactylidae as recently defined [Knoll, 2000].

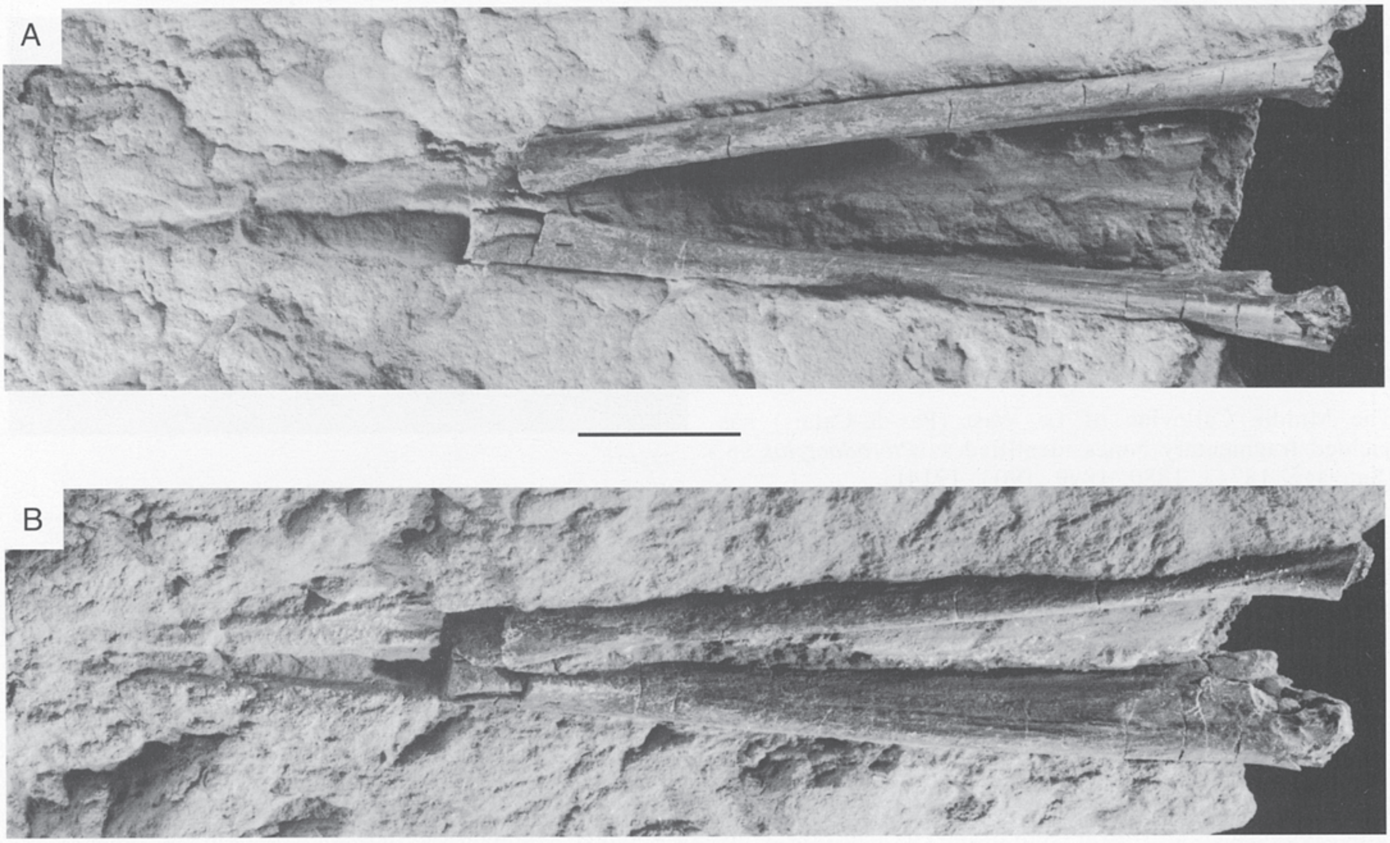

FIG. 2. – Pterosaurian mandible (? Pterodactylidae) from the Upper Jurassic (Tithonian) of the Boulogne-sur-Mer area (Bouveur collection, Saint-Omer). A : ventral view; B : oblique ventral view. Scale : 30 mm.

FIG. 2. – *Mandibule de ptérosaure (Pterodactylidae ?) du Jurassique supérieur (Tithonien) du Boulonnais (Collection Bouveur, Saint-Omer).* A : *vue ventrale ;* B : *vue ventrale oblique. Echelle : 30 mm.*

Fabre [1981] erected the subfamily Gallodactylinae to include *Gallodactylus canjuersensis*, *Cycnorhamphus suevicus* and *Diopecephalus longicollum*. Such a group would be paraphyletic but *Cycnorhamphus suevicus* and *Gallodactylus canjuersensis* indeed appear to form a clade [Jouve, 2000]. Bennett [1996a, p. 336], ignoring Fabre [1981], considers that there is 'general agreement' that *Cycnorhamphus suevicus* and *Gallodactylus canjuersensis* are, in fact, congeneric. According to Bennett [1996a, 1996b], *Diopecephalus longicollum* should be referred to as *Pterodactylus longicollum* whereas *Gallodactylus canjuersensis* should be referred to as *Cycnorhamphus canjuersensis*. With regards to the first proposed combination, it should be remarked firstly that, following the results of Jouve [2000], only the type-species of *Pterodactylus*, *Pterodactylus antiquus*, should be retained in this genus. Secondly, in the morphometric analysis of Atanassov and Strauss [2000], *Diopecephalus longicollum* consistently plotted with *Cycnorhamphus suevicus* rather than with other taxa and this was considered by these authors as suggesting close relationships. With regards to the second proposed combination, the absence of teeth in the species from Canjuers suggests that the genus *Gallodactylus* is justified.

The assignment of the pterosaur jaw from the Lower Tithonian of the Boulogne-sur-Mer area to any known species or genus is not possible. The specimen might document a new pterodactyloid taxon but due to its fragmentary condition, it appears at best, in the present classification of the Pterosauria, as a possible Pterodactylidae gen. et sp. indet.

SURVEY OF THE FRENCH PTEROSAUR RECORD

It must be underlined here that several possible but uncertain pterosaur remains (such as teeth), awaiting careful study, are not listed herein. Due to the uncertain systematic position of many specimens, the material is presented here following a stratigraphical order.

Rhaetian

Godefroit [1997] figured an incomplete tooth from the late Triassic of Varangeville (Meurthe-et-Moselle, northern France) and identified it as aff. *Eudimorphodon*. *Eudimorphodon* is indeed present in the famous site of Saint-Nicolas-de-Port (Meurthe-et-Moselle), four kilometres south of Varangeville [Godefroit and Cuny, 1997].

Hettangian

In several of his publications, O. Terquem (see e.g. Terquem [1855] and Terquem and Piette [1868]) reported the discovery in the Hettangian of Hettange-Grande (Moselle, northern France) of rare, fragmentary, flattened and hollow bones he doubtfully attributed to *Pterodactylus*. These bones (see figures in Gervais [1848-52 and 1859, Pl. 51, Figs 14-18]), originally kept in the private collection of O. Terquem in Metz (Moselle), were referred to as Pterosauria *incertae sedis* by Wellnhofer [1978]. They are, nevertheless, even doubtfully diagnostic at this level and some of them, at least may belong to (a) theropod(s) (cf. Cuny [1993]). One of these bones in particular [Gervais, 1848-52 and 1859, Pl. 51, Fig. 18], seems to be relatively too thickly walled for a pterosaurian bone and was finally regarded by Terquem [1855] as that of a theropod. The possible discovery of pterosaur remains in the Hettangian of the eastern Paris Basin has been evoked more recently [Maubeuge, 1955; Maubeuge and Delsate, 1997].

Callovian

The Middle Callovian of Le Wast (Pas-de-Calais) has yielded fragmentary bones identified as *Pterodactylus* sp. [Sauvage, 1874a, 1880, 1899, 1903, 1914].

The marine marl of Oxfordian (Marnes de Villers) and especially Callovian (Marnes de Dives) age from the Vaches Noires cliffs (Calvados, northern France) have yielded numerous vertebrate remains, especially mesosuchians. The collection of the Laboratoire de Paléontologie of the Muséum national d'Histoire naturelle (Paris) includes a pterosaur tooth (fig. 3), along with crocodilian teeth labelled as 'Une dent de ptérodactyle et dents du *Steneosaurus Heberti* [sic]. Callovien de Villers. Trouvé par M. Morel de Glasville' (number of entry 1890-13). This specimen, a possible 'Rhamphorhynchoidea', is rather reminiscent of rostral teeth of the German Lower Jurassic genus *Dorygnathus* [Arthaber, 1921], the dentition of which was quite developed, and some other Rhamphorhynchidae [Wellnhofer, 1975]. Still unpublished rhamphorhynchoid remains from the same locality can be added to this record [Bülow, pers. comm. to F.K., 1999].

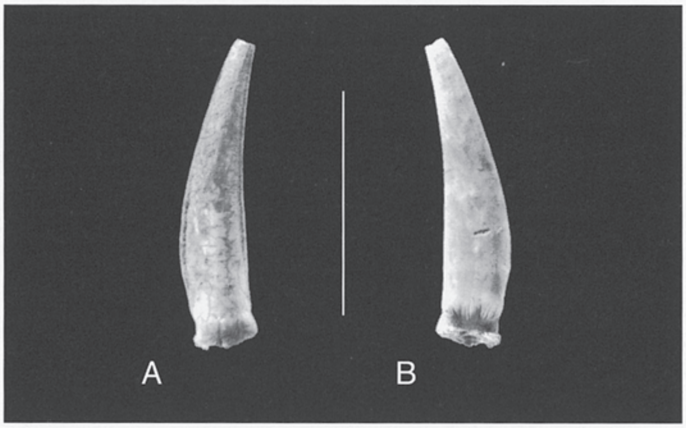

FIG. 3. – Isolated pterosaurian tooth (? Rhamphorhynchidae) from the Jurassic (Callovian) of the Vaches Noires cliffs (Muséum national d'Histoire naturelle, Paris). A : (?) labial view; B : (?) lingual view. Scale : 20 mm.
FIG. 3. – *Dent isolée de ptérosaure (Rhamphorhynchidae ?) du Jurassique (Callovien) des falaises des Vaches Noires (Muséum national d'Histoire naturelle, Paris).* A : *vue labiale (?)* ; B : *vue linguale (?). Echelle : 20 mm.*

Oxfordian

The Upper Sables de Glos (Upper Oxfordian), in the Lisieux area (Calvados), have yielded incomplete, elongated, hollow bones as well as teeth only referred to as Pterosauria [Buffetaut *et al.*, 1985; Milsent, 1986]. A photograph of one of these teeth (kindly provided by C. Milsent) shows a compressed and recurved specimen consistent with the morphology of a 'rhamphorhynchid' tooth. The presence of 'Ptéranodon' [sic] at Glos [Rioult and Leguillochet, 1995, p. 13] is therefore by no means correct.

Kimmeridgian

The marine Kimmeridgian layers surrounding the Cape de la Hève (Seine-Maritime, northern France) have yielded a small fragmentary limb bone referred to the genus *Pterodactylus* [Lennier, 1867, 1887] at Bléville (kept in the L. Boutillier collection of Roncherolles, Seine-Maritime). Among the vertebrates of the Poulain collection kept in the Musée cantonal de Géologie of Lausanne, Lepage [1996] listed a pneumatised bony fragment of a pterosaurian from the Lower Kimmeridgian of the Cap de la Hève.

More recently, Buffetaut *et al*. [1998] have reported the discovery of a number of pterosaur remains in the Kimmeridgian clay of the Cap de la Hève. Among this material are post-cranial bones apparently belonging to 'rhamphorhynchoids' and, moreover, an interesting specimen consisting of the associated upper and lower jaw (Musée Géologique Cantonnal, Lausanne, nº 59'583) of what appears to be a new Germanodactylidae, *Normannognathus wellnhoferi.* However, on one hand, following the analyses of Bennett [1996b], *Germanodactylus* may be a younger synonym of *Pterodactylus*. On the other hand, according to the recent cladistic analysis of Jouve [2000], the species of *Germanodactylus* form a paraphyletic group as well as those of *Pterodactylus*. So this is probably the case of the group (*Germanodactylus*, *Normannognathus*), as already suggested by Unwin and Heinrich [1999]. Be that as it may, the name Germanodactylidae [Young, 1964] should not be used any more. *Normannognathus wellnhoferi* is here ranked in the Dsungaripteridae [Young, 1964], which can be defined here, according to the results of Jouve [2000], as : *Germanodactylus rhamphastinus*, *Dsungaripterus wei*, their most recent common ancestor and all descendants (node-based taxon).

In 1873, Sauvage [1873] founded the new species, '*Pterodactylus*' *suprajurensis*, based on a partial coracoid, a portion of humerus and two fragmentary wing bones. According to him, this large species is probably the same as that suspected by Lennier [1867]. All the material comes from the same biostratigraphical zone (Autissiodorensis zone) of the Boulogne-sur-Mer area (Pas-de-Calais) but has been collected by different people. Sauvage [1874a] used the same combination in a following paper, but he later expressed doubt about the generic position of the species which would belong to 'un genre particulier' [Sauvage, 1880]. Sauvage [1894] changed once more his opinion before, finally, reallocating this species to *Rhamphorhynchus* [Sauvage, 1902, 1903, 1914]. The same species was also cited in the Eudoxus zone of the Boulogne-sur-Mer area [Sauvage, 1899, 1903, 1914], maybe from a long bone fragment, firstly attributed to the *Morinosaurus typus* [Sauvage, 1874b, Pl. 1, Fig. 5] of the same author and then to *Pterodactylus* sp. [Sauvage, 1880]. In fact this bone, which has disappeared [Vadet and Rose, 1986], does not particularly evoke that of a sauropod as *Morinosaurus typus* was in Sauvage's eyes (actually, this taxon should be regarded as a *nomen dubium* of quite enigmatic systematic allocation [Buffetaut and Martin, 1993]). '*Pterodactylus*' *suprajurensis* may be a *nomen dubium*, the type series of which must be considered as lost [Vadet and Rose, 1986].

More recently, some thin-walled bones, as well as a tooth, of pterosaurian (? rhamphorhynchid) affinities have been recovered by one of us (A.B.) in the Upper Kimmeridgian of the Boulogne-sur-Mer area.

The Upper Kimmeridgian of Fumel (Lot-et-Garonne, southern France) has revealed some bony fragments identified by Sauvage [1902] as an undetermined 'Ptérodactylien', smaller than '*Pterodactylus*' *suprajurensis* [Sauvage, 1873].

In the mid-nineteenth century Thiollière [1850] signalled the discovery at Cerin (Ain, southern France) of a bone 'de la jambe ou du bras d'un Saurien' before sending the specimen to H. von Meyer who immediately recognised it as the right humerus of *Pterodactylus* [Meyer, 1852]. Later, Meyer [1860] made this piece the holotype of the new species '*Pterodactylus*' *cirinensis* whereas Gervais [1871] listed a 'Ptérodactyle, d'espèce indéterminée' in the material from Cerin housed in the museum of Lyon. Lortet [1892] also assigned to the above species a probable tibia and referred a radius to '*Pterodactylus*' *grandis*, owing particularly to its large size. Both these bones also come from Cerin, as well as the ulna of a small pterodactyloid studied by Buffetaut *et al*. [1990]. The lithographic limestones of Cerin could be late Kimmeridgian – early Tithonian age [Enay *et al*., 1994].

Tithonian

Besides the large mandible described above, the Lower Tithonian near the 'Cran aux Œufs' (Pas-de-Calais) has yielded some other interesting specimens. Amongst them are a (?) 'rhamphorhynchid' tooth, a somewhat large but incomplete cervical vertebra and what appears to be a wing metacarpal IV, all of them housed in a private collection [A. B., pers. obs., 1999].

The Lower Tithonian of the 'Causses du Quercy' has yielded pterodactyloid teeth and isolated bones (one of them large) but, above all, pterodactyloid and 'rhamphorhynchoid' trackways [Lange-Badré, 1998; Lockley and Meyer, 2000 ; Mazin, 2000; Mazin *et al*., 1997; Mazin *et al*., 1998; Mazin *et al*., 1999; Mazin *et al*., 1995]. In this respect, the work of the Université de Poitiers at the Crayssac site (Lot, southern France), in which 'des empreintes de pattes d'oiseau' have been cited as early as 1978 [Obereiner, 1978], is fundamental. Indeed, it confirms the conclusions of Stokes [1957], namely the quadrupedal locomotion of the pterosaurs (see Mazin *et al*. [1995]). This locality has delivered at least three *Pteraichnus*-type ichnotaxa of pterodactyloid interpretation and rare tracks of 'Rhamphorhynchoidea' indet. [Mazin *et al*., 1995].

The Lower Tithonian of the Haute-Marne (northern France), has yielded a remarkable skull (housed at the Musée de Saint-Dizier under the inventory number 75-1671) of *Ctenochasma* [Taquet, 1972; Jouve, 2000].

The 'Pterodactylidae nov. de grande taille' [Ginsburg and Mennessier, 1970] from Canjuers (Var, southern France) is not Berriasian in age, as believed by Fabre [1977, 1981] and Fabre *et al*. [1982] but more probably early Tithonian (cf. e. g., Atrops [1994]). The pterosaur from Canjuers (Muséum national d'Histoire naturelle CNJ-71) is unique and the specimen was thus chosen as the holotype of a new species : *Gallodactylus canjuersensis* [Fabre, 1974, 1976]. Numerous tracks (including probably sphenodont ones) have been discovered at Canjuers but not fully described, it is not impossible that those of pterosaurs exist among them.

A layer of probably uppermost Tithonian age [Cuny *et al*., 1991], in the old quarry of Montrouge (Pas-de-Calais), has yielded a pterosaur tooth and three metacarpal epiphyses (Rose collection, Samer, Pas-de-Calais).

Hauterivian

The Lower Cretaceous of Haute-Marne (northern France) has yielded several limb bones of pterosaurs [Augé *et al*., 1992]. However, amongst them only a proximal ulna fragment from the Hauterivian of Attancourt could be described, as *Ornithocheirus* sp. [Buffetaut and Wellnhofer, 1983]. This specimen seems to have been first identified as the long bone of a wader [Cornuel, 1886] and is not determined beyond the rank of Pterosauria by Unwin *et al.* [2000].

Albian

The Lower Albian near Louppy-le-Château (Meuse, northern France) has yielded a remarkable cervical vertebra of possible ornithocheirid affinity [Barrois, 1875a, 1875b; Corroy, 1922; Sauvage, 1882a, 1882b] but not determined beyond the rank of the taxon Pterosauria by Unwin *et al.* [2000].

A close stratigraphical level at Grandpré (Ardennes, northern France) yielded six teeth (housed at present, like the vertebra mentioned above, in the Musée d'Histoire naturelle de Lille) referred to the same taxon as the above vertebra [Barrois, 1875b; Sauvage, 1882a, 1882b]. However, according to Buffetaut and Wellnhofer [1983], these would be of doubtful pterosaurian derivation because of their strong carinae.

Sauvage [1882b, 1909] also listed *Ornithocheirus compressirostris* in the Gault of the northeastern Paris Basin but this record seems dubious.

More recently, the Middle Albian of Le Gaty (Aube, northern France) has produced a similar specimen to the Louppy-le-Château vertebra. The specimen was identified as *Ornithocheirus* sp. by Buffetaut *et al*. [1989] but, more prudently, as Ornithocheiroidea by Unwin *et al*. [2000].

The Albian of the Boulogne-sur-Mer area has yielded pneumatised bones as well as teeth of ornithocheirid affinities (Bouveur collection, Saint-Omer).

Coniacian

The Décocq collection housed in the Musée d'Histoire naturelle de Lille [Anonymous, 1875] keeps pterosaurian material mentioned by Barrois [1874, 1875b] as '*Pterodactylus giganteus*'. This author has identified the specimen as a probable tibia and Gosselet [1881] estimated the original wingspan of the individual as over two meters. It has been found in the 'Craie blanche, niveau à *Micraster cortestudinarium*' of Lezennes-Lez-Lille (Nord, northern France) on August 18th, 1873. The old subterranean quarries of Lezennes exploited the Grey Chalk of Coniacian age [Monciardini *et al*., 1980]. Regarding the original description of Bowerbank [1846], the determination of the specimen as the tibia of the rather poorly known *Ornithocheirus giganteus* seems very uncertain (moreover, the type material comes from the Cenomanian).

Campanian

Graves [1847] noted the existence of 'ornitholites' (cf. Gervais [1844]) in the White Chalk (Lower Campanian [Blondeau *et al.*, 1974]) of Notre-Dame-du-Thil (Oise, northern France). According to Gervais [1859, p. 403 and 472]) these fossils (long bones fragments) may have belonged, in fact, to 'Ptérodactyles'. Unfortunately, the traditional chalk exploitation has ceased for a long time at Notre-Dame-du-Thil and there is thus no hope to renew such a casual discovery there.

Maastrichtian

In the terminal Cretaceous of southern France [Buffetaut, 1997; Buffetaut *et al.*, 1996; Buffetaut *et al.*, 1997; Laurent, 1996; Le Loeuff and Buffetaut, 1995], some pterosaurian bones have been found in the Lower Maastrichtian of Campagne-sur-Aude (Aude) and Upper Maastrichtian of Fontjoncouse (Aude) and Mérigon (Ariège). The material is rather fragmentary (mainly elongated hollow bones) but a very large incomplete cervical vertebra does seem to attest the presence of the family Azhdarchidae.

DISCUSSION AND CONCLUSION

As one can see, the French pterosaur record, contrary to the dinosaur one [Buffetaut *et al.*, 1991] appears, except perhaps for the terminal Jurassic (Kimmeridgian-Tithonian), rather poor. However, it seems interesting to examine more closely the pterosaur occurrence in France in relation with the stages of the Mesozoic era.

A graph presenting such a relation would show its acme in the Jurassic (Kimmeridgian-Tithonian) and two minor peaks in the Cretaceous (Albian and Maastrichtian). The scientific value and significance of this figure would, nevertheless, be rather limited. The graph would be principally biased by secondary factors (see below) and would merely reflect statistically the discovery of pterosaur fossils in France from different horizons up to now. Due to the poor record every new discovery would be able to change the distribution that is thus meaningless and essentially incidental.

Yet, it is remarkable to note that these three increased pterosaur concentrations perfectly correspond to those of the dinosaurs globally : Kimmeridgian – Tithonian, Albian – Cenomanian, late Campanian – Maastrichtian. These were times of high sea level, which favoured the fossilisation of such terrestrial animals [Haubold, 1990]. Moreover, the Jurassic peak of the French pterosaur record is partly linked to the particular deposits of the Kimmeridgian (Cerin) and the Tithonian (Crayssac, Canjuers) in which, however, pterosaurian bones are not common in absolute. Effectively, due to their peculiar skeletal characteristics (and, possibly, their mode of life), pterosaurs tend to be preserved in exceptional types of fossils localities ('Lagerstätten effects', see Buffetaut [1995]). Moreover, the peak of the Albian might be correlated with the long duration of this stage. Finally, the Maastrichtian tetrapod sites are by far the most numerous, the richest and the best excavated ones in France.

On the contrary, Unwin [1987], plotting species diversity against time, shows a major peak in the Kimmeridgian and a less important one in the Albian – Cenomanian times, but a gradual 'decline' from the Coniacian to the Maastrichtian.

In fact, many methodological biases hamper the study of the evolution of palaeobiodiversity and this is especially true for pterosaurs. The ghost lineages cannot be considered in this instance since the reconstruction of the phylogeny of pterosaurs (especially 'rhamphorynchoids') remains very problematical. In fact, owing to the reasons exposed above, it appears quite illusory to estimate the actual pterosaur diversity during the Mesozoic and it should even be recognised that this group would tend to pervert such studies when these are of more inclusive level. Thus, the apparent diversity through time of pterosaurs, 'incontesta- blement, de tous les êtres [de l'ancienne existence], les plus extraordinaires' [Cuvier, 1824, p. 379], is unsuitable to bring arguments, in either one way or another, to the mass extinction debate.

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